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Short communication

Application of compound interest laws in biology: Reunification of existing models to develop seed bank dynamics model of annual plants

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ABSTRACT

Reunification of widely-usedclassic models in ecology is a very important step for the field to grow. In this study, classic models based on compound interest law, which exists in many natural phenomena, were reunified, and a seed bank dynamics model of annual plants was developed.

We found an intrinsic relationship between the compound interest of unit period and density dependence, and the relationship was interpreted using evolutionary stability strategies of a single seed. Based on the relationship, a seed bank dynamic model of annual plants was constructed, and compound interest of the unit period and discrete-time dynamic processes, by which a new density-dependence based on the benefit balance of storage and investment (defined as the compound interest law) was derived.

Our model not only can be used to reunify the three classic models (Cohen's, Goldberg's, and Bulmer's) but can also support different levels of density dependence in the seed bank dynamics of annual plants. Our study has shown that the compound interest law interprets seed bank dynamics more clearly than the traditional power law, not only because there are close relationships between the compound interest law and the power laws in numerical simulations but also because the compound interest law can be directly interpreted by the evolutionary stability theory.

Our study provides new insight into the bet hedging theory and the life-history evolution of plants with seed banks by adding a compound interest term to the fitness function of annual plants. We suggest that if the interest rate of delaying growth can be defined by compensating for delayed growth, compound interest of the unit period will play an important role in biology and ecology.

1. Introduction

Many natural phenomena follow the compound interest law. Compound interest has important applications in human society based on the benefit of storage and investment in economics (Almenberg and Gerdes, 2012). A compound interest model of annual growth and increases in dry weight was proposed by Blackman back to 1919 (Blackman, 1919). The law of compound interest has been used frequently in other fields, but its development in biological and ecological theory has been slow (Connolly et al., 2001; Erickson, 1976; Hember et al., 2012).

The key to compound interest research primarily lies in the organism's choice of interaction characteristics on different temporal and spatial scales (Fischer and Fiedler, 2002). Three formulas for compound interest exist in terms of different periods of time: (1) continuous compound interest e^{rt} (where r is the growth rate and t is the time) (Blackman, 1919; Shimojo et al., 2010); (2) compound interest of k periods $(1+r)^k$ (where r is the interest rate and k is the number of periods); continuous compound interest as well as compound interest for k periods has received more attention in evolutionary ecology (Weis et al., 2000); (3) compound interest of a unit period $(1+r/k)^k$ (where r is the interest rate and k is the amount of deposit interest added to the principal).

We found here that the storage compound interest of the unit period was more relevant to individual growth than are

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other factors. However, this finding must be tested on theoretical grounds.

Seed dormancy is an important life cycle strategy that improves the sustainability of populations in fluctuating environmental conditions. Plant species growing in rapidly fluctuating environments must be preserved in permanent soil seed banks to prevent extinction (Gutterman, 2002). The possibility of seasons with zero seed production is low but not zero. This behavior is called delayed germination at the seed level. Seeds in any soil seed bank have only a limited chance of germination, even if the conditions for germination are perfect. Thus, soil seed banks must be permanent. Many different models have been used to illustrate this phenomenon from an evolutionary viewpoint (Cohen, 1966; Bulmer, 1984; Ellner, 1985; Gutterman, 2002; Kuang and Chesson, 2009).

An obvious trade-off exits between plant yield and germination (Rees, 1993, 1994). The first seed bank dynamic model of annual plants, called Cohen's model, was proposed in 1966 (Cohen, 1966).

$$S(t+1) = S(t)[gf(gS(t))H(t) + (1-g)(1-d)], \quad (1)$$

where $S(t)$ is the number of seeds in the soil bank during season t; $H(t)$ is the average yield of each plant in season t; g is the total germination ratio; and d is the death rate of dormant seeds. $f(x)$ represents the density dependence function, and $x = gS(t)$ indicates the number of seeds surviving after competing for germination. The first seed bank dynamics model of annual plants was proposed without considering density dependence, which mean that $f(x) = 1$ in Eq. (1).

Cohen's model was gradually improved. Two main strategies have been used, both of which focus on density dependence. The first was proposed by Bulmer et al. (Bulmer, 1984; Ellner, 1985; Thomas, 1993; Valleriani, 2005; Tielbörger and Valleriani, 2005). $f(gS(t) = Q/[Q + gS(t)]$ in Eq. (1), where Q is the carrying capacity of the system, specifically the maximum density of adult plants supported by the environment. This equation is based on the reciprocal yield law, as first proposed by Shinozaki and Kira (Shinozaki and Kira, 1956; Firbank and Watkinson, 1985). The second strategy was proposed by Goldberg et al. (Goldberg, 1990; Kuang and Chesson, 2009). $F[gS(t)] = e^{-cS(t)}$ in Eq. (1), where c defines the total effect of competition on reproductive fitness of each individual. It is based on the exponent yield law, as proposed by Ricker (Ricker, 1954).

It is necessary to determine if there exists some intrinsic links among the three models. At present, the density-dependence law is mostly based on power laws (Farazdaghi and Harris, 1968; Holliday, 1960; Yoda et al., 1963; Watkinson, 1980; Antonovics and Levin, 1980; Deng et al., 2012) and the reciprocal yield law (see Appendices A and B for more details) (Willey and Heath, 1969; Hassell, 2000). There is an error in the reciprocal yield law, which is mentioned in Appendix A. There have been a lot of efforts to derive mechanistic explanations of these and related power laws in ecology (see Li et al. (2000) for some related discussion and references). There is still no good, general interpretation of these power laws, even they fit experimental data well (Antonovics and Levin, 1980; Deng et al., 2012).

We first noticed that compound interest of the unit period of one seed plays an important role in permanent soil seed banks. We tackled this idea, which was an extension of classic seed bank models, by adding a compound interest term to the fitness function of annual plants and constructed a seed bank dynamic model of annual plants for one seed, with compound interest of the unit period and discrete-time dynamic processes. Our results show that the density dependence can be interpreted by the evolutionary stability theory, mainly because one seed can choose germination or no germination so that there is an evolutionary stability strategy.

2. Model construction and derivation

Symbols and explanation of the model parameters and their derivation

$H(t) = H$ where H is the average yield of each plant during season t;
$S(t)$ is the number of seeds in the soil bank during season t;
S is the stable number of seeds in the bank;
g is the total germination ratio;
d is death rate of dormant seeds;
$f(x)$ represents the density dependence function;
x, $N = gS(t)$ indicates the number of surviving seeds after germination competition;
Q is the carrying capacity;
Y is the total yield of all plants in a season.
k is the amount of deposited interest added to the principal and the average of the occurrence of number of compensation (reproductive success) opportunities in a unit period.
a is the nongermination interest rate of nondormant seeds, which is based on seeds that can benefit from nongermination by preserving their chance of germination for some future date, when conditions may be more favorable.
C and D are constants in the power law.
b is a proportionality factor (dimensionless).

The relationships and intrinsic links between the three existing models are open to question. The density-dependence law must be experimentally determined, but no unified mechanism by which these laws may be interpreted has yet been published. Here, compound interest was important to the permanent soil seed banks. The intrinsic links between the three seed bank dynamic models of annual plants and the compound interest of density dependence as interpreted by the evolutionary stability strategies of one seed are shown.

It is hypothesized that the seed is homogeneous, the germination proportions have ceased to change, the germination ratio is evolutionarily stable, the soil seed bank is stable, and $S(t+1) = S(t) = S$, and $H(t) = H$, where H is the average yield of each plant during the season t (Bulmer, 1984; Ellner, 1985).

g is the total germination ratio, and d is the death rate of dormant seeds. Here, we give another interpretation for g and d. $d(1-g)$ is loss of soil seed bank in a cycle, $d(1-g)+g$ is the germinating part, where $d(1-g)$ can be seen as seeds die before becoming seedlings, and only g seeds become seedlings (see Fig. 1). So $d(1-g)$ can also be defined as the death rate of germinated seeds.

Seeds benefit from germination, but they also benefit from not germinating. Thus, the germination decision of each seed should be considered.

Delaying germination and avoiding the risk of extinction in hedge bets theory essentially addresses the issue of how to maximize interest by storing seeds for future germination. Seed nongermination and economic storage interests are essentially the same. Seeds benefit from not germinating by preserving their chance of germination for some future date when conditions may be more favorable. Here, if the germination rate of one seed is 1, a is defined as the nogermination interest rate of nondormant seeds or interest rate. If the germination rate of one seed is g, then ga is interest rate of the seed.

The so-called interest, which can stimulate or inhibit seed production, is the potential future benefit. The interest rate of nondormant seeds is determined by the carrying capacity Q and the number of seeds in bank S. The optimized nongermination interest rate of nondormant seeds should be consistent with seed production. When Q is large, a low nongermination interest rate stimulates seed production. When S is large, large delays occur in germination,

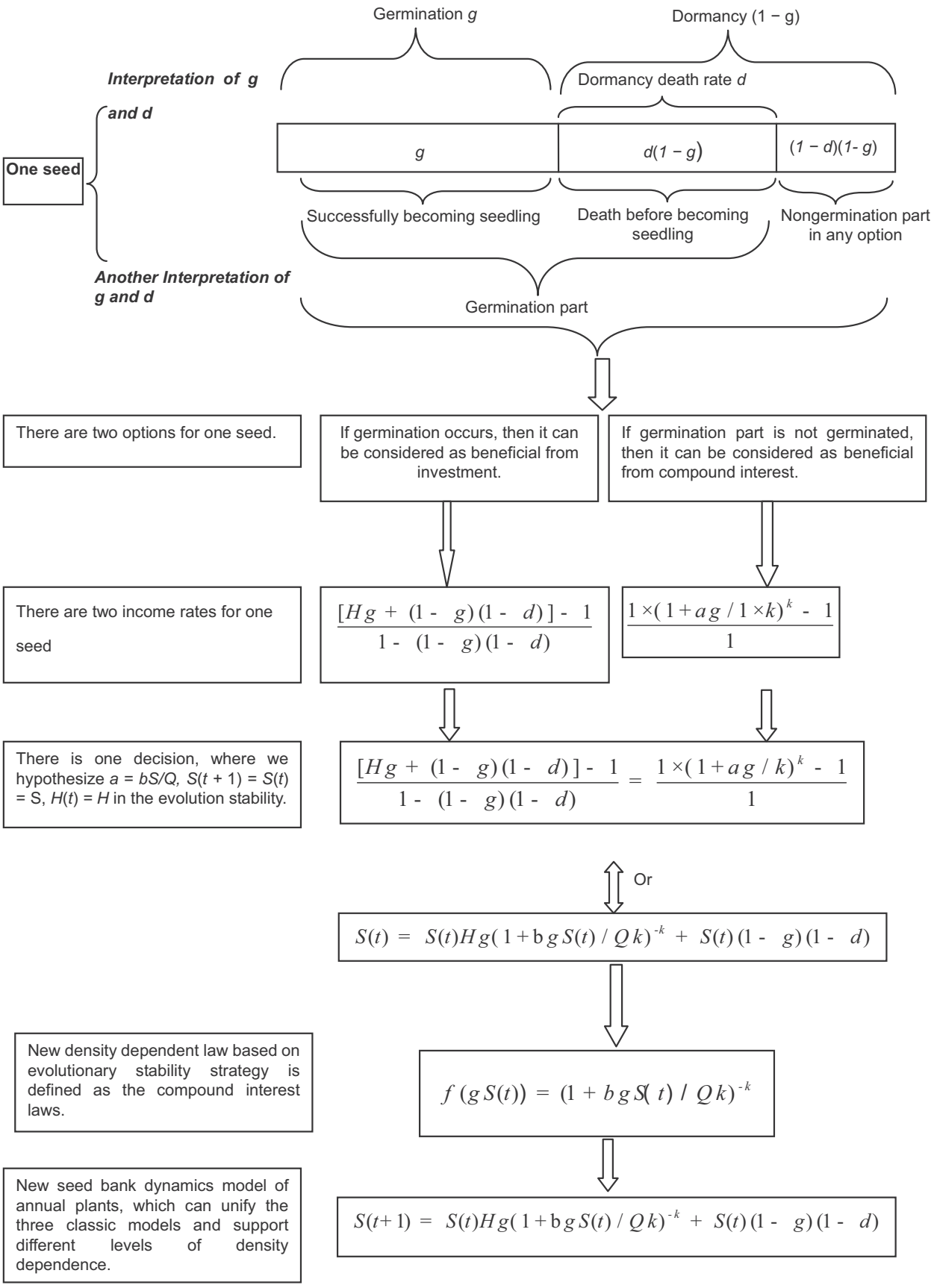

Fig. 1. Seed bank dynamic model of annual plants based on compound interest laws.

which can inhibit seed production. This results in $a = bS/Q$. Here, b is a proportionality factor (dimensionless).

Two options are available per given unit period for seeds in which the germination rate is g. One option is germination. The compound interest for the unit period of nongermination is $[(1+ag/k)^k - 1]/1$, where k is the amount of deposited interest added to the principal (the number of compensation occurrences in a unit period), and $1/k$ is the risk of delayed germination. The other option is nongermination. The net yield of germination is $[(1-g)(1-d)+gH-1]$, and the investment of germination is $[1-(1-g)(1-d)]$. The units of expected investment income rate are defined as $[(Hg+(1-g)(1-d)]-1)/(1-(1-g)(1-d)]$.

When the opportunity of germination is less than the interest period for each unit period, germination will not occur. When delayed germination interest is less than the opportunity for the profit of germination, delayed germination will not occur. The germination ratio is an evolutionarily stable strategy, so seed germination profit is equal to the compound interest of nongermination (Bishop–Cannings theorem; Broom et al., 1997). This gives the following equation (see Fig. 1):

$$\frac{[Hg+(1-g)(1-d)]-1}{1-(1-g)(1-d)} = \left(1+\frac{ag}{k}\right)^k - 1, \quad a = \frac{bS}{Q} \tag{2}$$

From Eq. (2), we obtain Eq. (3) as follows:

$$S(t) = S(t)Hg\left(1+\frac{bgS(t)}{Qk}\right)^{-k} + S(t)(1-g)(1-d) \tag{3}$$

From Eqs. (1) and (3), $S(t+1)=S(t)$; the left side is $S(t+1)$, and the second part of the right side is old seed. Thus, the first part of the right side is new seed from the season t. Because $S(t)gH$ is the total yield without density-dependence, we define $f[gS(t)] = [1+bgS(t)/Qk]^{-k}$ as density-dependent.

If $N = gS(t)$ and $b=1$, $f[gS(t)] = [1+bgS(t)/Qk]^{-k}$ can also be rewritten as $f(N) = (1+N/Qk)^{-k}$, $f(N) = (1+N/Qk)^{-k}$ is defined as the compound interest law of density dependence. The compound interest law can be directly interpreted by evolutionary stable theory.

The so-called density-dependent effects of competition are of interest to many researchers. From Eq. (3), the more density-dependent the effects of competition are the greater the expected return on investment when the benefits and risks are stable. Density dependence is the reciprocal of the investment return from seed production.

3. Unified model and its comparison with others

Density dependence before the seed bank becomes stable is given in Eq. (4):

$$S(t+1) = S(t)Hg\left(1+\frac{bgS(t)/Q}{k}\right)^{-k} + S(t)(1-g)(1-d) \tag{4}$$

The second part of the right side of Eq. (4) is old seed, and the first part of the right side of Eq. (4) is new seed from season t with density dependence $[1+bgS(t)/Qk]^{-k}$. Thus, the left side is $S(t+1)$.

Eq. (4) unifies the three classic seed bank dynamics models of annual plants (Cohen's, Goldberg's, and Bulmer's). (a) If $k \to 0$ (which means that the risk is very large), Sg/Q is a constant function, and no detectable density dependence occurs. Eq. (4) is Cohen's equation (Cohen, 1966). (b) If $k \to +\infty$ and $b/Q = c$ (which indicates almost no risk), the compound interest of delayed germination e^{cSg} is equal to the germination income, and density dependence is e^{-cSg}. Eq. (4) is Goldberg's equation (Goldberg, 1990). (c) If $k \to 1$ and $b=1$, then the compound interest of delayed germination $(1+Sg/Q)$ is equal to germination income, and density dependence is $1/(1+Sg/Q)$. Eq. (4) is Bulmer's equation (Bulmer, 1984; Ellner, 1985). The three types of yield laws (Cohen's, Goldberg's, and Bulmer's) have been unified by the law of compound interest.

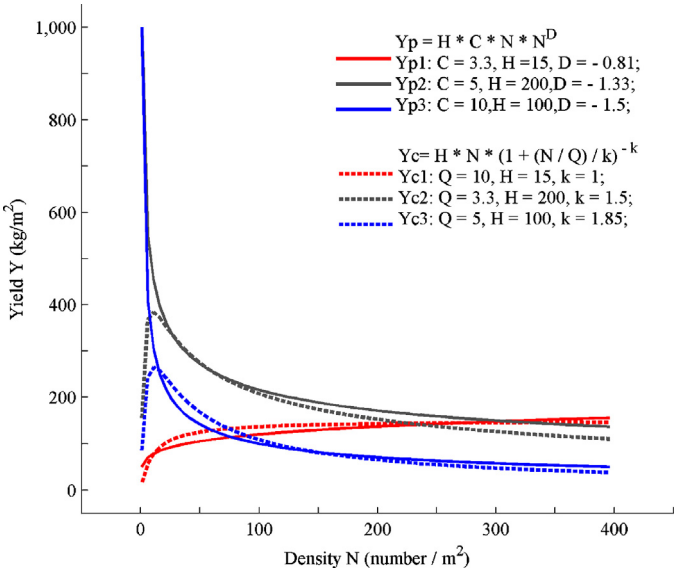

Fig. 2. Comparison of numerical simulations of the seed bank model based on the power law. ($Y/N = HCN^D$) and the compound interest law ($Y/N = H(1+N/Qk)^{-k}$).

Eq. (4) supports different levels of density dependence among seed banks. Because there is only one opportunity for annual plants to breed each year, the amount of deposited interest added to the principal is one unit. Thus, $k=1$ is successfully used in Bulmer's equation for the density dependence of annual plants. However, because of rapidly fluctuating external environmental conditions, 1 year usually contains more (or less) than one opportunity to breed successfully, so k may be greater (or lesser) than 1.

The density-dependent law (see Appendices A and B) is mostly based on power laws derived from a large number of experiments (Holliday, 1960; Yoda et al., 1963; Farazdaghi and Harris, 1968; Watkinson, 1980; Deng et al., 2012), and the power laws match well with experimental data. But why is there no good interpretation of those power laws?

Here we offered an alternative explanation. We compared the power laws ($Y/N = HCN^D$) from the previous classic studies (Holliday, 1960; Yoda et al., 1963; Farazdaghi and Harris, 1968; Watkinson, 1980) and the compound interest laws [$Y/N = H(1+N/Qk)^{-k}$] through numerical simulation (see Fig. 2), where H is the average yield of each plant; C and D are constants in the power laws; Y is the total yield of all plants during a season; Q is the carrying capacity; and k is the amount of deposited interest added to the principal and the occurrence of average number of compensation (reproductive success) opportunities in a unit period. For comparison purpose, the definition of $R^2_{F,G}$ is as follows:

$$R^2_{F,G} = \frac{\left(\sum_{i=1}^{80}((F(i5) - \frac{1}{80}\sum_{k=1}^{80}F(5k)) * (G(5i) - \frac{1}{80}\sum_{j=0}^{80}G(5j))\right)^2}{\left(\sum_{i=1}^{80}\left(F(5i) - \frac{1}{80}\sum_{i=1}^{80}F(5i)\right)^2\right)\left(\sum_{i=1}^{80}\left(G(5i) - \frac{1}{80}\sum_{i=1}^{80}G(5i)\right)^2\right)} \tag{5}$$

When N is not very small (bigger than 10, $R^2_{Y_{P1},Y_{C1}} = 0.924$, $R^2_{Y_{P2},Y_{C2}} = 0.934$, $R^2_{Y_{P3},Y_{C3}} = 0.968$), there is a close relationship between the power and compound interest laws. Seed bank dynamics are more clearly interpreted by compound interest laws because of the evolutionary stability strategy.

4. Discussion and conclusion

In this paper, we offered a new insight into bet hedging theory and the life-history evolution of plants with seed banks. The intrinsic link between the compound interest of the unit period and density dependence can be interpreted using the evolutionary stability strategies of a single seed. We extended classic seed bank models by adding a compound interest term to the fitness function of annual plants and constructed seed bank dynamic models of annual plants for one seed, compound interest for the unit period, and discrete-time dynamic processes.

It is more reasonable to start from a single seed selection as opposed to directly from the soil seed bank for soil seed bank dynamics modeling. Almost all studies on the seed bank modeling mention those three models, many of which are based on the original and expanded into a different space, environment, and time. There are many developments based on the classic seed bank models, which directly begin modeling from the soil seed bank (Thomas, 1993; Andrea and Eva, 2002; Tielbörger and Valleriani, 2005; Mathias and Chesson, 2013). One of the greatest novelties in our model is that we derived seed bank dynamics starting from an individual seed. Following this idea, we obtained density dependence based on evolutionary stability and also provided the general seed bank dynamic model.

From our modeling, we observe that a single seed approach gives better results than a soil seed bank approach. Although natural selection is acting on the individual, the results are reflected at the population level. Adaptation of populations is achieved through individual decisions during the process of natural selection. Through the model we established, we observed that the classic Eq. (1) can also be successfully interpreted from the perspective of a single seed. Therefore, the model derived using a single seed perspective is consistent with the classic model [Eq. (1)] established by considering the population as a whole, although the yield reciprocity law in Eq. (1) has a mechanistic interpretation. However, considering the fact that the parameters a and b are not constant (see Appendix A), this approach still has some imperfections. The single seed approach, which we developed using compound principles and evolutionary stability theory, includes unity and expansion for Eq. (1) and density-dependent laws.

The reunification of previous classic studies is very important for developing ecological theories (McGill et al., 2007). Our model can be used not only to reunify the three classic models (Cohen's, Goldberg's, and Bulmer's) but also to support different levels of density dependence in seed bank dynamics of annual plants. A single year usually contains more (or less) than one opportunity for successful breeding because of the fluctuating environmental conditions. The new parameter k, the amount of deposited interest added to the principal, is the average number of compensation (reproductive success) opportunity occurrences in a unit period.

The compound interest law is preferable to the power laws at least for annual plants, as shown in Fig. 2. We find that when N is not very small, there is a close relationship between the power and compound interest laws; on the other hand, when N is very small, the power laws are inaccurate, but the compound interest laws are accurate. This can be verified by comparisons with real data (Fig. 4 appearing in the "Models and tests of optimal density and maximal yield for crop plants" (Deng et al., 2012)). Therefore, compound interest laws agree well with experimental data whether N is big or small. Our study has shown that the compound interest law interprets seed bank dynamics more clearly than the traditional power law, not only because there are close relationships between the compound interest law and the power laws in numerical simulation (Fig. 2) and real date (Deng et al., 2012) but also because the compound interest law can be directly interpreted by the evolutionary stability theory. Although the power laws (Antonovics and Levin, 1980) can be used as a basis for subsequent analyses because of their ubiquity, potential uses, and lack of ambiguity (Stumpf and Porter, 2012), we suggest that the power law ($Y/N = HCN^D$) should be replaced by the compound interest law [$Y/N = H(1 + N/Qk)^{-k}$] as a more general modeling framework in biology and ecology.

Although compound interest for k periods and continuous compound interest has received attention (Blackman, 1919; Connolly et al., 2001; Erickson, 1976; Hember et al., 2012), the compound interest of a unit period has not been attended to in biological and ecological theories thus far. The compound interest of the unit period has a considerable direct influence on matters related to individual growth history, such as density dependence. One of the results of pursuing interest between different individuals in a unit period is closely related to the size of the storage compound interest of the unit period, in which there is considerable influence on individual investment options. This idea had been established by the reunification of annual soil seed bank models in which quantitative relationships among storage compound interest per unit period, population density dependence, and evolutionarily stable germination rate (individual investors) can be obtained.

The compound interest law of the unit period applies not only to annual plants but also to other ecological units. If an adult plant delays growth, there is compensation for delayed growth. The compensation can be defined as the rate of interest for delaying growth. Direct and indirect interactions among all plant characteristics throughout its life affect reproductive success regardless of whether the bulk of its energy is invested in seed germination, growth, reproduction, seed dormancy, or seed germination (Reekie and Bazzaz, 1992; Reekie et al., 2002; Koons et al., 2008). As long as storage is beneficial for plant growth, the compound interest of a unit period from storage occurs naturally. We believe that the role of compound interest in the unit period will be more important in future development of biological and ecological theories.

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Appendix A. The problem with the reciprocal yield law

A large number of models have been used to describe the relationship between plant density and the yield of a particular plant or plant part, but Willey and Heath (1969) singled out reciprocal equations such as those proposed by Farazdaghi and Harris (1968) and Holliday (1960) as most promising for describing yield–density relationships. Shinozaki and Kira (1956) first proposed that the mean total dry matter production per plant can be described by a reciprocal equation of this form.

Only the reciprocal yield law has a theoretical mechanism for the density-dependent part of the model, but there is a serious problem. The following description is given by Peterson and Higley (2000).

Willey and Heath (1969) provide a review of the functional forms to quantify yield–density relationships used through the 1960s. They concluded that the reciprocal equations are best suited for explaining these relationships because they are the only equations that can best explain both forms of the yield–density

relationship and because their parameters have some biological meaning.

Shinozaki and Kira (1956) derived reciprocal equations to explain yield–density relationships and made three very important assumptions.

First, the growth of a plant can be described by a general logistic curve:

$$\frac{dw}{wdt} = \lambda\left(1 - \frac{w}{W_{\max}}\right), \tag{A.1}$$

where λ is the intrinsic rate of increase in biomass, w is the biomass of an individual plant at time t, and $W_{\max}$ is the maximum attainable biomass of an individual plant. Following similar arguments as those used to derive the density-dependent growth equation, we obtain the following equation:

$$w = \frac{W_{\max}}{1 + ce^{-\lambda t}}, \tag{A.2}$$

where c is an integration constant. Both $W_{\max}$ and λ are assumed to be constant and independent of time and λ to be independent of density. We explicitly assume that the relationship between per unit biomass rate of growth (dw/wdt) and biomass of the individual is linear.

The second assumption of Shinozaki and Kira is critical. To this point, we have made arguments regarding the growth of a population (numbers of individuals) or of the biomass of an individual plant. The method used to describe crop yield (Y = biomass per unit area) in relation to population density was the elegance of their analysis. They assumed that the final yield per unit area (Y) of a plant in monoculture is constant and independent of density.

$$Y = W_{\max}N, \tag{A.3}$$

where N is the density. This is known as the law of constant final yield. Eq. (A.1) implies that at the time a plant reaches $W_{\max}$, the quantity of biomass in an area does not depend upon the number of individuals.

The third assumption made by Shinozaki and Kira is that all plants are simultaneously seeded at $t = 0$ and that average seed weight is constant and independent of density.

$$w_0 = \frac{W_{\max}}{1 + c} = \frac{Y/N}{1 + c} \tag{A.4}$$

$$c = \frac{Y}{w_0 N} - 1 \tag{A.5}$$

As mentioned earlier, c is a constant; thus, by substituting it back into Eq. (A.1), the reciprocal yield equation can be derived as follows:

$$\frac{1}{w} = a + bN, \quad \text{where} \quad a = \frac{e^{-\lambda t}}{w_0}, \quad b = \frac{1 - e^{-\lambda t}}{Y} \tag{A.6}$$

Eq. (A.6) shows that the relationship between the reciprocal of per plant yield and population density is linear.

This form of the reciprocal equation only explains the asymptotic relationship between yield and density in a monoculture. However, Kira et al. argued that the parabolic relationship can be explained using additional assumptions regarding plant allometry.

Shinozaki and Kira conducted further analyses where they relaxed the assumption that λ and $W_{\max}$ are independent of time. They showed that when λ or $W_{\max}$ are allowed to vary with time, the simple reciprocal yield Eq. (A.6) can be derived. However, under such conditions, a and b are redefined so that λ or $W_{\max}$ varies with time. Eq. (A.3) is solved for yield (Y) to quantify yield per unit area as a function of plant density (N):

$$w = \frac{N}{a + bN}, \tag{A.7}$$

where a and b are identical to that described above.

Shinozaki and Kira relaxed the assumption that λ and $W_{\max}$ are independent of time; thus, the foundation of Eq. (A.7) is not strict.

Appendix B. Response of the population to density

Antonovics and Levin (1980) reviewed that three phases can be recognized in the response of a population to density in experiments where plants were grown over a range of densities.

B.1. Low-density phase

At extremely low densities, individuals do not compete for resources. Increasing density has no effect on dry weight per plant but results in a direct linear increase in yield per unit area.

B.2. Medium-density phase

Plants generally respond to moderate density by reducing growth rate (and a consequent reduction in size and reproductive output). Yield per unit area rapidly approaches a constant value, equivalent to the "carrying capacity" of the area under consideration. The density–yield relationship takes the following form:

$$\frac{1}{w} = AP + B, \tag{B.1}$$

where w is the weight per plant, p is the density of plants sown, and A and B are species-specific constants. This is termed as the "density effect law."

B.3. High-density phase

Mortality effects become important at high densities. Mortality due to density effects within a pure stand is called "self-thinning." There is a different relationship called the "−3/2 power law of self-thinning (also called the −3/2 power rule or Yoda's law)" such that

$$w = CP^{-3/2}, \tag{B.2}$$

where w is the weight per plant, p is the density of surviving plants, and C is a species-specific constant.

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